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# Differences in swimbladder volume between Baltic and Norwegian spring spawning herring: possible consequences for mean target strength

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Volume and shape of the swimbladder of Baltic and Norwegian spring spawning herring were measured, together with individual herring fat content. Swimbladder size was found to differ significantly between the two herring stocks. The larger swimbladder volume of Baltic herring is suggested to be associated with the fish's low fat content, which may be linked to its specific energy budget and the low salinity of the Baltic Sea. A buoyancy model that considered the different salinity conditions and fat proportions was used to evaluate the observed differences in swimbladder volume. The swimbladder volume data were subsequently used to model the mean target strength (TS) as a function of depth and growth pattern. Backscattering of the swimbladder was modelled using the Modal-Based Deformed-Cylinder Model (MB-DCM), describing the swimbladder as a gas-filled elongated prolate spheroid. The fish body component was modelled as a fluid-filled ellipsoid using the Distorted Wave Born Approximation (DWBA). Modelling results support a different TS to size relationship for Baltic herring, with a stronger echo, due to the larger swimbladder. Depth and length dependent TS relationships based on the model results are suggested.

Keywords: Baltic herring, swimbladder volume, depth dependence, target strength.

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## Introduction

Biomass estimates determined from acoustic surveys for fish are dependent on accurate values of target strength (TS) for conversion of echo intensity into numbers of fish (Ehrenberg 1974; MacLennan 1990; Simmonds and MacLennan 2005). A fish's TS is a measure of its capacity to reflect sound and it is dependent on a range of variables including fish size (Love 1977; Nakken and Olsen 1977), tilt (Midttun and Hoff 1962; Love 1971; Nakken and Olsen 1977; Blaxter and Batty 1990), physiology (Ona 1990; Ona et al.

2001; Horne 2003), morphology (Jones and Pearce 1958; Foote 1980), depth (Ona 1990; Mukai and Iida 1996; Gorska and Ona 2003a, 2003b) and acoustic frequency (Haslett 1977; Foote 1985; Horne and Jech 1998, 1999). Nevertheless, present biomass evaluation from acoustic survey data is exclusively based on the relationship between TS and fish length (McClatchie et al. 2003).

Since the swimbladder is an important contributor to the total backscattered sound from a fish (Jones and Pierce 1958; Foote 1980; Blaxter and Batty 1990), it has been suggested to

include a depth factor into the TS relationship for herring and some other physostomes to account for swimbladder compression caused by increased pressure with depth (Blaxter and Batty 1990; Ona 2003; Gorska and Ona 2003a, 2003b; Fässler et al. 2007). The physostomous herring do not have a gas gland and their swimbladder is connected to both the alimentary canal and the anal opening. There is a general consensus that herring “gulp in” air at the sea surface to inflate their swimbladder and cannot therefore refill the swimbladder once they have left the sea surface and started to descend (Brawn 1962; Blaxter et al. 1979; Ona 1990; Nero et al. 2004). Consequently, the herring swimbladder can be expected to compress at increasing water pressures in accordance with Boyle’s law, leading to a steady decrease in TS with increasing depth. This has also been confirmed experimentally by measurements of swimbladder volumes at 30 m depth (Ona 1990), and later acoustically by *in situ* and *ex situ* experiments (Ona 2003).

In some cases differences in the physical environment may influence the behaviour and also the physiology and morphology of the fish, resulting in increased intra-species variation in TS. For instance, Baltic herring were found to have 3-7 dB higher average TS values than herring living in the North Sea (Lassen and Stæhr 1985; Rudstam et al. 1988; Didrikas and Hansson 2004; Peltonen and Balk 2005). This variation was linked to the fundamentally different environments the fish are living in, resulting in different morphological adaptations. The Baltic Sea has a low salinity when compared to north-east Atlantic waters (approx. 7 and 35 PSU, respectively) and Baltic herring were found to have a much lower fat content (~2-15%) than both Norwegian spring spawning and North Sea herring (~15-25%) (Huse and Ona 1996; Cardinale and Arrhenius 2000; Ona et al. 2001; Aidos et al. 2002; Kiviranta et al. 2003). In order to maintain neutral buoyancy the swimbladder has to counterbalance the weight of the fish body to match the density of the surrounding sea water. Fat has a lower density than sea water and can therefore contribute to positive buoyancy as well (Brawn 1969). For these reasons it has been argued that Baltic herring may have larger swimbladders, leading to the higher average TS values observed (Didrikas and Hansson 2004).

Swimbladder morphology data from surface adapted Baltic and Norwegian spring spawning

herring were used to determine whether there were any differences in morphological adaptations between herring living in environments that differ in salinity. Size of the swimbladder necessary to give the fish neutral buoyancy was estimated assuming typical fat content and salinity conditions specific to both herring stocks. A backscattering model was used to examine the effect of the differences in swimbladder volume on the TS of herring. The Distorted Wave Born Approximation (DWBA; Dezhang Chu, Woods Hole Oceanographic Institute, USA, pers. comm., 2005) was used to model the fish body as a fluid-filled ellipsoid. The swimbladder was modelled as a gas-filled elongated prolate spheroid using the Modal-Based Deformed-Cylinder Model (MB-DCM; Stanton, 1988, 1989). Based on the modelling results new depth and length based TS relationships are proposed for both Norwegian spring spawning and Baltic herring. Results are compared to current and previous versions of TS relationships available for Atlantic herring.

## Materials and methods

### *Swimbladder morphology*

Swimbladder morphology data of Baltic herring were collected at Forsmark nuclear power plant, on the Swedish east coast north of Stockholm in 1988. In order to prevent damage to internal organs the fish were caught close to the surface by land seines and were allowed to swim freely to a 5 m<sup>3</sup>, 1 m deep holding tank at the experimental site. The fish were held in the holding tanks where they were allowed to adapt to surface pressures for 7-10 days. Immediately before swimbladder volume measurements the herring (number of samples n = 104) were scooped over to a smaller tank in batches of 5 and 5, where they were anaesthetised with 300‰ benzocaine. The swimbladders of the strongly anaesthetised fish were emptied by gentle ventral massage from beneath the pelvic fins towards the anal opening. Swimbladder gas was collected with an inverted funnel, which was suspended beneath the water with a top mounted glass burette. Swimbladders were effectively emptied by underwater dissection and their volume measured to the nearest 0.1 ml. No residual gas was found in the main chamber or the anal duct after inspection. Each fish was weighed to the nearest 1 g and its length measured to the nearest

0.1 cm. Eventually, all fish samples were analysed for percentage fat content by standard methods using Na<sub>2</sub>SO<sub>4</sub> grinding and ethyl ether extraction (see Brawn 1969). Results were then compared to swimbladder volumes of Norwegian spring spawning herring (published in Ona 1990) collected in 1983 at Skogsvaag in western Norway, using the same methods.

Assessment of measured swimbladder volumes was attempted under the assumption that herring aim to minimise energy expenditure by maintaining a state of neutral buoyancy (i.e. the density of the whole fish has to equal the sea water density). For the fish to gain neutral buoyancy, the swimbladder has to acquire a certain volume ( $V_{sb}$ , in %) relative to the whole fish volume in order to balance the density of the surrounding sea water ( $\rho_{sw}$ ) and fish body ( $\rho_{fish}$ ):

$$V_{sb} = \frac{\rho_{fish} - \rho_{sw}}{\rho_{fish} - \rho_{sb}} \quad (1)$$

The density of the swimbladder gas ( $\rho_{sb}$ ) was assumed to be 0.0013 g•cm<sup>-3</sup> (Brawn 1969). Sea water density was calculated according to an algorithm developed by Fofonoff and Millard (1983) using an equation of the form  $\rho_{sw} = \rho(T, S, z)$ , where the density is a function of temperature (T), salinity (S) and depth (z). Uniform values for temperature of 10°C and salinity of 35 PSU were assumed for the Norwegian Sea. Values of 10°C and 7 PSU were respectively chosen for the Baltic Sea. Density of the fish body ( $\rho_{fish}$ , i.e. whole fish excl. swimbladder) was calculated using an adapted proportion key for volumes of various body components determined by Brawn (1969) for Pacific herring (*Clupea pallasii*):

$$\begin{aligned} &\text{fat : scales : bones : "rest"} \\ &= [V_f] : [0.5] : [1.2] : [98.3 - V_f] \end{aligned} \quad (2)$$

The density of the fish body was then calculated by dividing the sum of the weighed densities (volume proportion × density) of each body component by the sum of all body volume proportions. Fat contents ( $V_f$ ) were based on measurements of the collected herring samples (Norwegian spring spawning herring: mean = 18.4%; Baltic herring: mean = 7.3%). Considering the steadily decreasing trend in fat content of herring in the Baltic proper since the

early 1980s (Cardinale and Arrhenius 2000), current values were based on recent findings of Bignert et al. (2007) and were assumed to be 2.1%. Swimbladder volume estimates for Baltic herring were performed using both the 1980s and current fat content values. The following density values were used according to data published by Brawn (1969): fat, 0.926 g•cm<sup>-3</sup>; scales, 1.966 g•cm<sup>-3</sup>; bones, 1.993 g•cm<sup>-3</sup>; and the “rest”, 1.057 g•cm<sup>-3</sup>. In that way swimbladder proportions of total fish volume could be estimated theoretically for both Norwegian spring spawning and Baltic herring cases. Conversion to absolute volumes was done by calculating the volume of the fish body by dividing the weight by the density ( $\rho_{fish}$ ). Predicted model and observed empirical values were compared using correlation analysis.

#### Target strength modelling

A theoretical backscattering model was used to estimate the mean TS of herring. The output of the model was the mean backscattering cross-section  $\langle \sigma_{bs} \rangle$ , averaged over geometrical and acoustic parameters, which was converted to TS according to MacLennan et al. (2002):

$$TS = 10 \log_{10} \langle \sigma_{bs} \rangle \quad (3)$$

The model consisted of two separate components that were combined to give a total for the whole-fish backscatter: the fish body was modelled as a fluid-filled ellipsoid and the swimbladder as a gas-filled elongated prolate spheroid. The term ‘fish body’ describes all parts of the body (flesh, bones, scales, organs) except the swimbladder. Total backscattering cross-section was then expressed according to Gorska and Ona (2003b) by

$$\sigma_{bs}^f = \sigma_{bs}^{sb}(z) + \sigma_{bs}^b \quad (4)$$

where  $\sigma_{bs}^b$  and  $\sigma_{bs}^{sb}(z)$  denote the backscattering cross-section of the fish body and the swimbladder at a depth  $z$ , respectively.  $\sigma_{bs}^f$  describes the backscatter of the whole fish. Assuming that fish flesh material properties are similar to the surrounding sea water, the fish body component was modelled using a Distorted Wave Born Approximation (DWBA) model developed by Dezhong Chu (Woods Hole Oceanographic Institute, USA, pers. comm.,

2005). Details of the model routines can be found in Fässler et al. (2007). The Modal-Based Deformed-Cylinder Model (MB-DCM) used to model the swimbladder is described in Gorska and Ona (2003a).

Assumptions about ellipsoid dimensions of the fish body model were based on X-ray images of herring (Norwegian spring spawning herring: E. Ona, unpublished data; Baltic herring: N. Håkansson, F. Arrhenius, B. Lundgren, pers. comm.). The ratio of fish length to lateral height was 5.3. The ratio of fish length to dorsal width was 8.0 for Norwegian spring spawning and 10.7 for Baltic herring. Density and sound speed contrasts were 1.04 and 1.04 for the fish body and 0.00129 and 0.23 for the swimbladder, respectively. The modelled swimbladder was assumed to be 0.26 times the total length of the fish (Gorska and Ona 2003a). The remaining dimension (width) of the prolate spheroid was adjusted to give measured swimbladder volumes for a given fish length for both Norwegian spring spawning and Baltic Sea herring. The herring swimbladder volume decreases with depth according to Boyle's law (Ona 1990) and swimbladder dimensions were assumed to contract with depth in the following manner:

$$a(z) = a(0)(1 + z/10)^{-\alpha} \quad (5)$$

$$b(z) = b(0)(1 + z/10)^{-\beta} \quad (6)$$

$a$  and  $b$  describe the width and length of the prolate spheroid, respectively. Boyle's law requires the compression factors  $\alpha$  and  $\beta$  to behave according to  $2\alpha + \beta = 1$ . TS were evaluated for extreme cases of contraction rates, i.e. maximum:  $\alpha = 1/3$ ,  $\beta = 1/3$ ; and minimum:  $\alpha = 1/2$ ,  $\beta = 0$  (see Gorska and Ona 2003a). According to Gorska and Ona (2003a, 2003b) and based on fish morphology (Blaxter 1979; Ona 1990) the second case (minimum contraction rates) is more realistic and was consequently used to estimate TS relationships.

To account for the tilt dependent directivity pattern of the swimbladder, the simple solution for a straight cylinder was used (Medwin and Clay 1998). The angle between the swimbladder and snout-tail axis was ignored. A Gaussian orientation distribution (fish tilt angle  $\theta$ ) with a mean of  $0^\circ$  and S.D. of  $5^\circ$  was used for all calculations. Consequently, backscattering characteristics averaged over fish orientation

were determined and TS values could be calculated for a variety of fish lengths and depths. Length and depth dependent TS relationships at 38 kHz were determined and compared to *in situ* TS data of Norwegian spring spawning herring (Ona 2003).

## Results

### *Swimbladder morphology*

Surface adapted Baltic herring had significantly larger swimbladder volumes for a given fish weight (probability ( $p$ ) for differences between slopes:  $p < 0.001$ ) when compared to Norwegian spring spawning herring (Figure 1). Based on linear regression slopes swimbladder volumes of Baltic herring (slope = 0.057) were on average about three times as big as those of Norwegian spring spawning herring (slope = 0.017, see Ona 1990), for fish that weigh more than 44.25 g. Due to the lower intercept of the regression line fitted to the Baltic herring data, spring spawning herring that were lighter than 44.25 g on average had a larger swimbladder compared to Baltic herring. However, confidence intervals of estimated swimbladder volumes did overlap at these low weights, making potential differences insignificant.

Correlation analysis suggested small differences between empirically determined swimbladder volumes and modelled values assuming neutral buoyancy of the fish (Figure 2: Norwegian spring spawning herring: correlation coefficient  $r = 0.937$ , probability  $p < 0.001$ ; Baltic herring:  $r = 0.901$ ,  $p < 0.001$ ). The highly significant correlations for both herring cases is not surprising since the slopes of the lines fitted to the theoretically determined swimbladder volumes for a given weight (Norwegian spring spawning herring: 0.020; Baltic herring: 0.056) were nearly identical to the ones of the lines fitted to the empirical data (Figure 1). This would also suggest that the input parameters of the swimbladder model (salinity and herring fat content) were appropriate and sufficient to describe the empirical data. If current fat content percentages were used, the model suggested that swimbladder volumes of Baltic herring would be 18% larger than what they were at the beginning of the 1980s. For that reason and to reflect current conditions, recently observed values of fat content were used to adjust measured

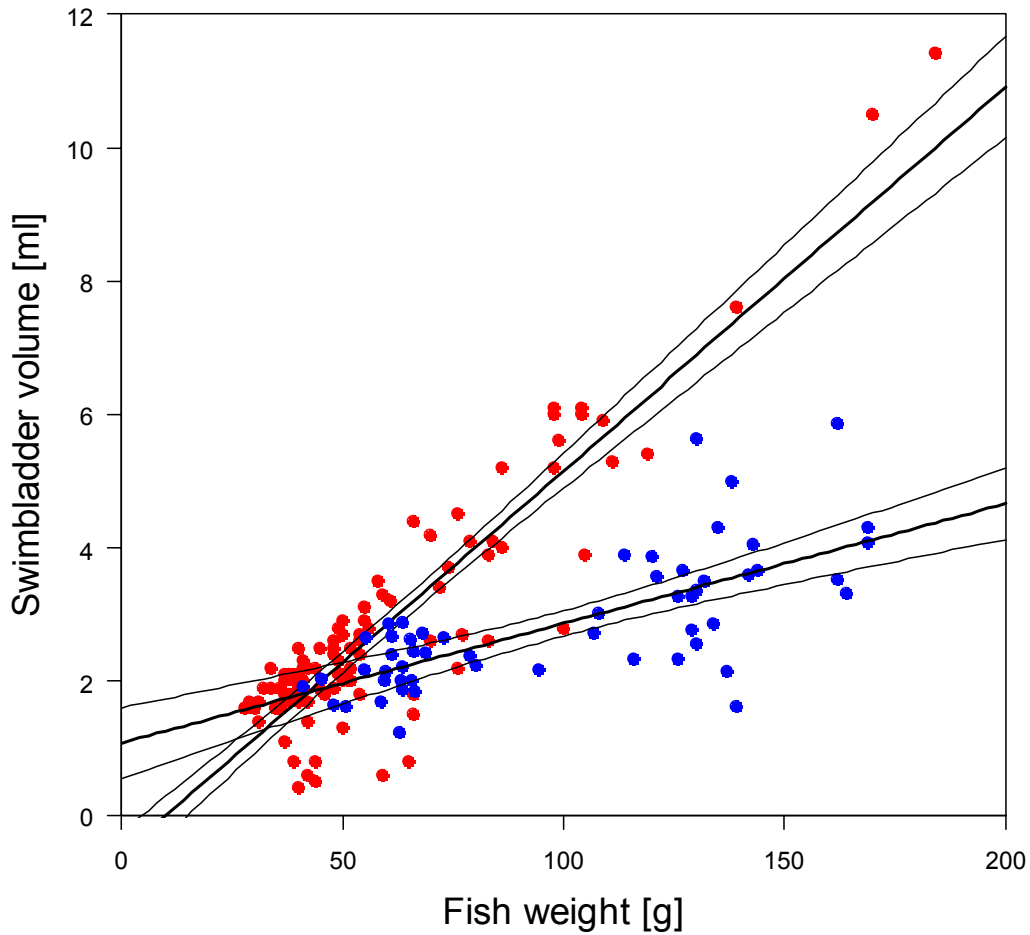


Figure 1. Swimbladder volume in relation to fish size for Baltic (red) and Norwegian spring spawning herring (blue) collected between 1982 and 1985. Regression lines with 95% confidence intervals are given. Baltic herring:  $y = 0.057x - 0.59$ ,  $n = 104$ ,  $S.E. = 0.77$ ,  $R^2 = 0.82$ . Norwegian spring spawning herring:  $y = 0.017x - 1.18$ ,  $n = 60$ ,  $S.E. = 0.66$ ,  $R^2 = 0.77$  (see Ona 1990).

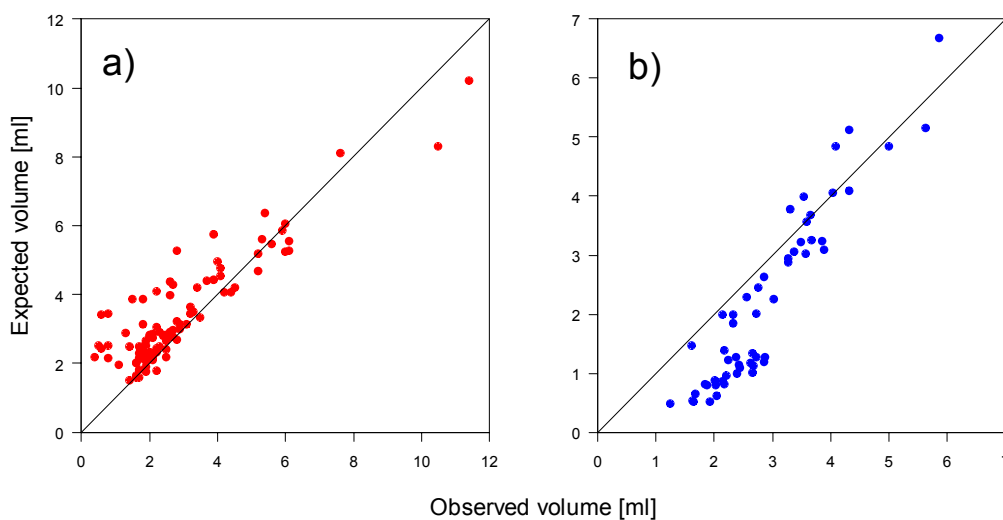


Figure 2. Correlation between observed and expected swimbladder volumes for (a) Baltic herring and (b) Norwegian spring spawning herring. Expected volumes are based on observed fat contents of the fish and typical salinity values of Baltic (7 psu) and north-east Atlantic waters (35 psu).

swimbladder volumes for subsequent TS modelling.

### Target strength modelling

Incorporating swimbladder volumes from measured herring samples (Figure 1) into the TS model allowed computation of backscattering strength values for a range of depths and fish sizes for both Baltic and Norwegian spring spawning herring. Figures 3a and 4a represent contour plots of modelled TS values assuming minimum contraction rates ( $\alpha = 1/2$ ,  $\beta = 0$ ), i.e. the swimbladder length did not change with increasing water depth. The model revealed higher TS values for Baltic herring, especially so for large fish ( $\geq 30$  cm), where differences of  $\sim 2$  dB were observed.

Degrees of change in total TS with depth were not consistent among fish sizes for both Baltic and Norwegian spring spawning herring (Figures 3a and 4a). The oscillating nature of the averaged fish body backscatter estimated by the DWBA modelling method resulted in some fish size ranges being more influenced by the backscatter of the fish body as opposed to the swimbladder (i.e. the fish sizes corresponding to the maximum of the oscillating fish body averaged backscattering cross-section). This was

especially true for Norwegian spring spawning herring of 22.5-27.5 cm (Figure 3b) and Baltic herring of 26-31 cm (Figure 4b). For these fish sizes the total TS variation was about 1.5-2.0 dB. On the other hand, Norwegian spring spawners of 15-22.5 cm and  $>30$  cm, and Baltic herring of 18-23 cm were less influenced by the fish body backscatter (i.e. the fish sizes corresponding to the minimum of the oscillating fish body averaged backscattering cross-section). At these sizes the total TS variation was about 2.5-3.0 dB. We demonstrated that the variability of TS with depth depends on the fish body contribution to the total backscatter of the fish.

To bring the modelled TS values into context a comparison to *in situ* observations of Norwegian spring spawning herring published in Ona (2003) was done. Narrow length distributions of observed herring in Ona's (2003) investigation enabled his measured TS to be normalised to a common fish size of 32 cm. Consequently, models were run for fish of that size for both Norwegian spring spawning and Baltic herring cases. Estimated mean TS values for both herring races were within the range of most *in situ* TS values apart from a few low values at shallow water depth (Figure 5). Since the empirical measurements were based on a

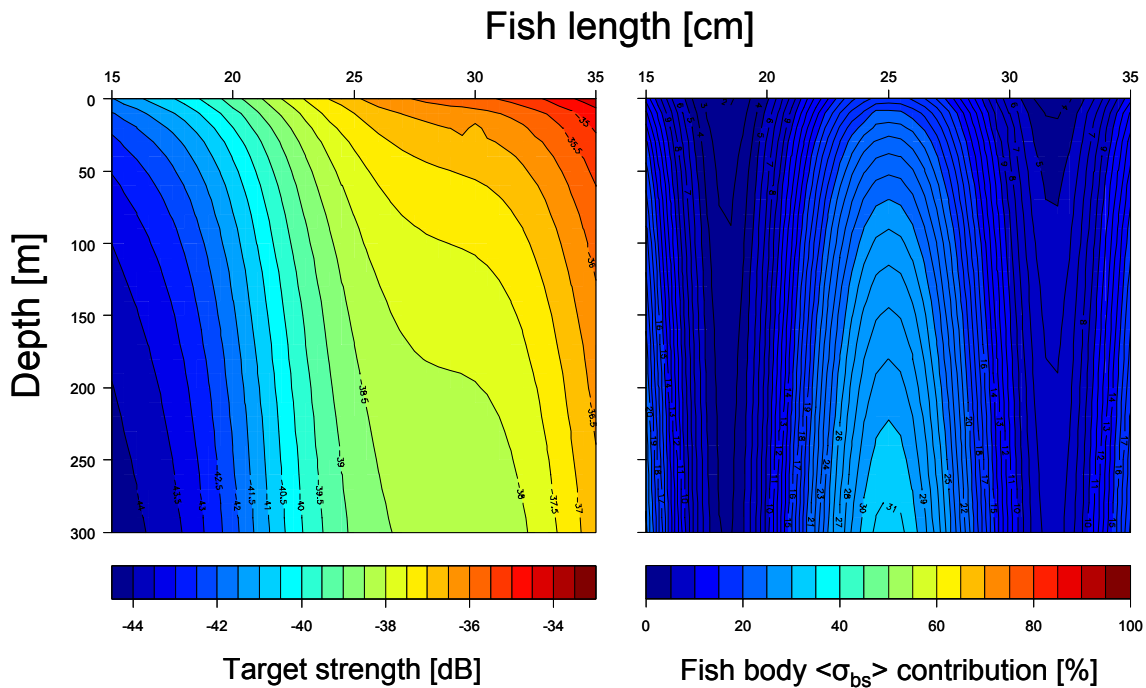


Figure 3. Depth dependence of the modelled mean target strength (left panel) of Norwegian spring spawning herring at 38 kHz and the body contribution to the total backscatter of the fish (right panel). Swimbladder dimensions were assumed to contract with depth according to compression factors  $\alpha = 1/2$  and  $\beta = 0$ .

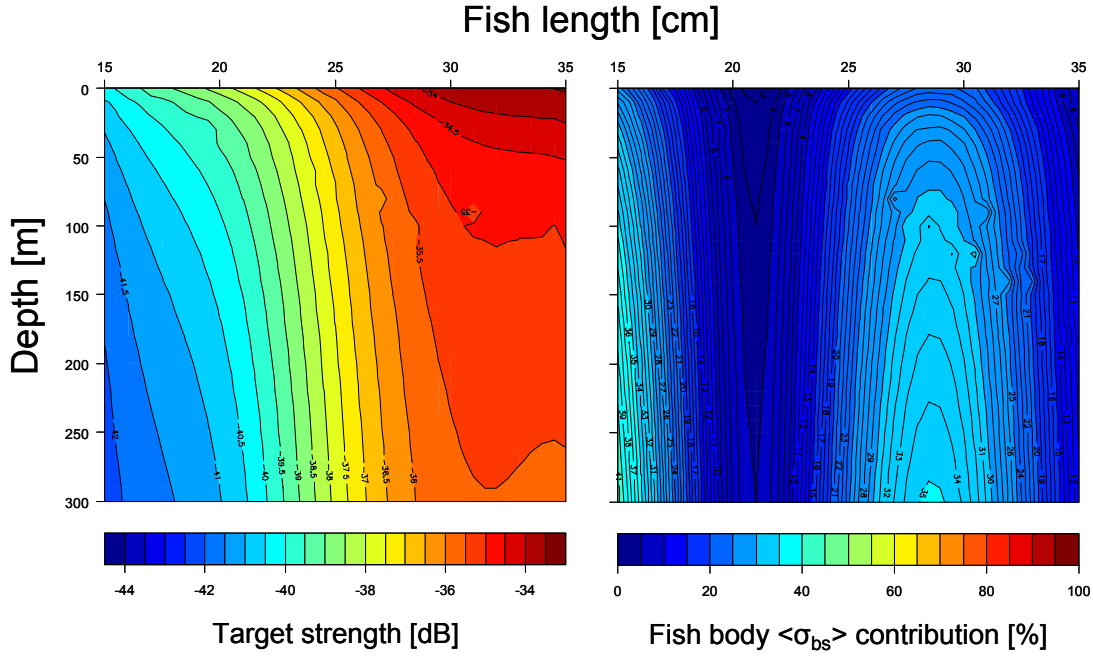


Figure 4. Depth dependence of the modelled mean target strength (left panel) of Baltic herring at 38 kHz and the body contribution to the total backscatter of the fish (right panel). Swimbladder dimensions were assumed to contract with depth according to compression factors  $\alpha = 1/2$  and  $\beta = 0$ .

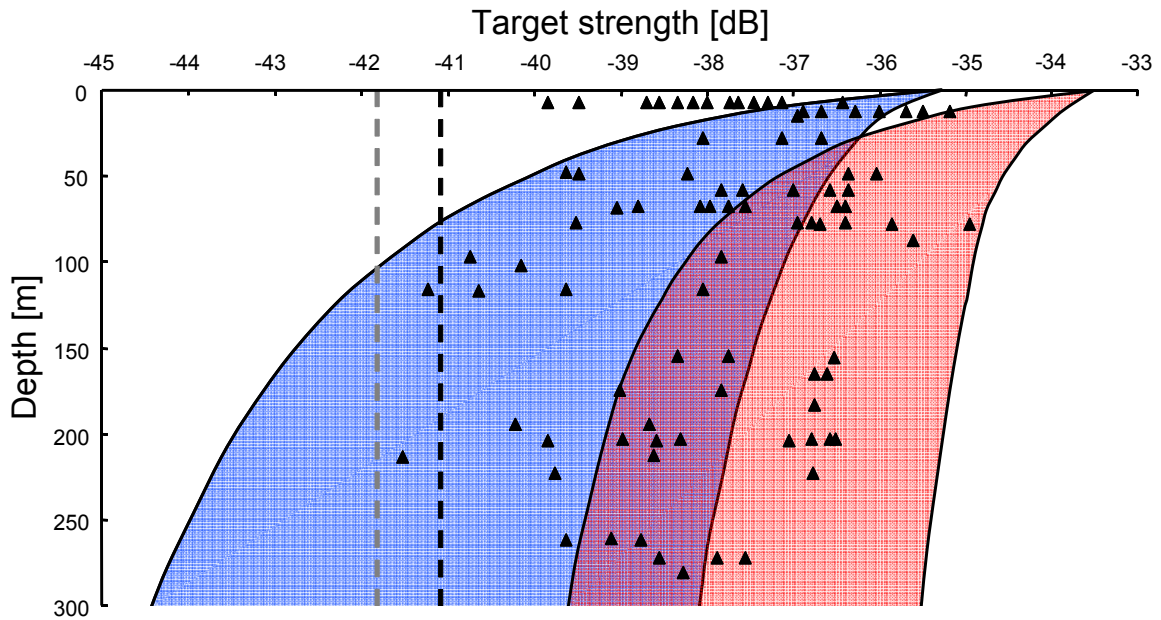


Figure 5. Modelled depth dependent mean target strength values for Baltic (red shaded area) and Norwegian spring spawning (blue shaded area) herring compared to measured *in situ* values for Norwegian spring spawning herring (Ona 2003) standardised to a fish size of 32 cm (black triangles). Borders of the shaded areas are defined by the extreme cases of swimbladder contraction rates, i.e. assuming maximum ( $\alpha = 1/3$ ,  $\beta = 1/3$ ) and minimum ( $\alpha = 1/2$ ,  $\beta = 0$ ) compression factors, respectively. Length based target strength relationships currently used for stock assessment are drawn as dashed lines for both Norwegian spring spawning (grey) and Baltic (black) herring.



range of different experiments performed at various times of the year, it can be assumed that the measured herring expressed differences in density, behaviour and condition. These factors can affect the measured TS (Ona 1990; Blaxter and Batty 1990; Ona et al. 2001; Ona 2003) and might therefore have resulted in the large spread observed in the empirical measurements throughout the depth range analysed. Modelled surface mean TS for Norwegian spring spawning herring were around 2 dB lower than those of Baltic Sea herring. Shaded areas in Figure 5 represent modelled TS values that fall between the extreme cases of swimbladder dimension contraction with depth, where the length compression factor was equal or less than that of swimbladder width. Mean TS values for Norwegian spring spawning herring throughout the water depth analysed ranged from -35.2 to -38.1 dB for minimum and from -35.2 to -44.4 dB for maximum swimbladder contraction rates. Similarly, values for Baltic herring ranged from -33.5 to -35.5 dB for minimum and from -33.5 to -39.5 dB for maximum contraction rates. Modelled mean TS values overlap in cases where high swimbladder compression factors are assumed for Baltic and low ones for Norwegian spring spawning herring. Most model and empirical TS estimates were stronger than the currently applied depth-independent length based TS relationships used for stock assessment (Figure 5).

Averaging the mean TS values for the entire water column analysed gave values for Norwegian spring spawning herring of -37.2 and -42.0 dB for the minimum and maximum contraction cases, respectively. The equivalent values for Baltic herring were -35.0 and -38.3 dB. The standard depth independent relationships between TS and fish length (L, in cm) obtained from these results assuming minimum swimbladder compression were:

$$TS = 20 \log_{10}(L) - 67.3 \quad (7)$$

for Norwegian spring spawning herring and

$$TS = 20 \log_{10}(L) - 65.1 \quad (8)$$

for Baltic Sea herring. Estimated intercepts in both equations are higher (Norwegian spring spawning herring: +4.6 dB; Baltic Sea herring: +6.1 dB) than the ones currently used for stock assessment of the respective stocks (Norwegian

spring spawning herring: see ICES 1988; Baltic herring: see ICES 1997).

Similarly, the length and depth dependent TS relationships fitted to the modelled mean TS data, in the form proposed by Ona (2003), were:

$$TS = 20 \log_{10}(L) - 1.9 \log_{10}(1 + z/10) - 65.2 \quad (9)$$

for Norwegian spring spawning herring and

$$TS = 20 \log_{10}(L) - 1.4 \log_{10}(1 + z/10) - 63.6 \quad (10)$$

for Baltic Sea herring.

## Discussion

Our study justified the existing assumption that due to the lower salinity in the Baltic Sea and their lower fat content, Baltic herring require a larger swimbladder volume for a given fish size when compared to herring stocks living in more marine salinity conditions. The analogy to larger swimbladder volumes in freshwater fishes (see Warner et al. 2002) seems clear. A larger swimbladder is a better reflector of acoustic energy. Modelling of the acoustic backscatter based on measured swimbladder volumes revealed higher mean TS for Baltic herring of a given length when compared to Norwegian herring (Figures 3a and 4a). These results may explain the TS values observed in central and northern Baltic herring (Didrikas and Hansson 2004; Peltonen and Balk 2005), which are 3-7 dB higher than those currently applied for both North Sea and Baltic herring.

Resulting TS values modelled for both Norwegian spring spawning and Baltic Sea herring at a range of water depths were comparable to *in situ* values at 38 kHz from Norwegian spring spawning herring collected by Ona (2003) (Figure 5). In fact, the length dependent TS equation determined for Norwegian spring spawning herring (Equation 7) is identical with the equivalent equation (Equation 4) published in Ona (2003), who based his findings on *in situ* values measured at various (5-500 m) depths. Model values determined for Baltic herring (Equation 8) are higher (+2.7 dB) than the ones proposed by Didrikas and Hansson (2004) at 38 and 70 kHz, and lower (-2.2 dB) than the ones determined by Peltonen and Balk (2005) for northern Baltic herring at 38 kHz.



Both of these investigations were based on *in situ* TS measurements. Nevertheless, it is generally suggested that both Baltic and Norwegian spring spawning herring have a higher TS than the one used to assess their respective stock. If the depth and length dependent TS relationships corresponding to the model values were used to estimate stock sizes, values would be lower than if the currently used solely length dependent TS relationships (i.e. Norwegian spring spawning herring:  $TS = 20\log_{10}(L) - 71.9$ ; Baltic Sea herring:  $TS = 20\log_{10}(L) - 71.2$ ) are used. Moreover, if the higher TS values for Baltic herring were correct and applied for the stock assessment, the Baltic herring biomass would be less than half as large (Didrikas and Hansson 2004). The same is correct for Norwegian herring, where corrections for vessel avoidance (Olsen et al. 1983; Vabø et al. 2002; Ona et al. 2007) were additionally introduced when the depth dependent TS relationship was applied for stock assessment. In the Baltic Sea, where most of the herring occur in shallow water, the effect of vessel avoidance is likely to cause a significant bias.

It should be noted that the model used in the present study is based on a highly simplified approximation of the herring swimbladder and fish body shape. It has previously been shown that the change in acoustic backscatter of herring with depth is dependent on the dorsal cross-section of the swimbladder rather than its volume (Ona 1990). Additionally, it is also more likely that the swimbladder diameter reduces more rapidly with depth than the length (Gorska and Ona 2003a). Given these results, improved knowledge about the true morphology of the swimbladder is needed to allow the usage of more sophisticated backscattering models. Therefore, precise measurements of swimbladder size and dimensions (e.g. using X-ray or MRI techniques) should be made at a range of water pressures in order to gain a better understanding about the mechanics of swimbladder compression. Improved, fully three-dimensional backscattering models, using techniques such as the Kirchhoff-ray mode (KRM; Clay and Horne 1994), should then be used to link the more precise morphological swimbladder dimensions to the expected TS.

## Conclusion

Based on measurements of swimbladder volumes of surface adapted Baltic and Norwegian spring spawning herring, it was found that the former have larger swimbladders for a given fish size. Modelling has shown that swimbladder volumes of herring are likely to depend on water salinity and fat content of the fish. Modelled mean TS values based on measured swimbladder volumes of Baltic and Norwegian spring spawning herring were larger for Baltic herring by about 2 dB. The backscattering model used suggested that the depth variability of TS is sensitive to fish size. The estimated TS-length relationships for both Baltic and Norwegian spring spawning herring revealed higher TS values for a given fish length than the relationships currently used to assess both stocks.

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